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Patterns of occurrence of semi-aquatic reptiles in highly invaded Mediterranean rivers

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Abstract

The fluvial systems in the north-east of the Iberian Peninsula are highly disturbed habitats, with widespread occurrence of alien species. Previous studies have shown that alien species have a major impact on native freshwater fauna, but it is not known what effect they have on semi-aquatic reptiles. Here the author investigated the factors that influence the occurrence of three species of semi-aquatic reptiles, one turtle (*Mauremys leprosa*) and two snakes (*Natrix astreptophora* and *Natrix maura*), at 261 sites in seven rivers/streams in Girona (north-eastern Spain). The studied semi-aquatic reptiles are habitat generalists which can occupy sections of rivers with altered regimes. The relationships of reptile presence to abiotic niche parameters and the presence of alien species were evaluated, as well as the patterns of pairwise co-occurrence between the reptiles. The presence of alien species did impact one out of three reptiles in this community. The association between both species of natricines was weakly negative, suggesting that interspecific competition does not structure their co-occurrences. The removal of alien species is the most appropriate strategy to preserve the complete diversity of native semi-aquatic reptiles.

Keywords

alien fishes, co-occurrence, *Mauremys*, *Natrix*, *Procambarus*, seasonal streams

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Introduction

The Mediterranean region has a high diversity of reptiles, including many endemic species (Sindaco and Jeremčenko 2008). This region has had dense human populations since historical times and its natural (particularly riverine) habitats have been subject to intense impacts (Corbacho et al. 2003; Ferreira et al. 2007). As a consequence of human activities, the populations of several semi-aquatic reptiles are in severe decline (Filippi and Luiselli 2000; Cox et al. 2006). This is attributable to a decline in habitat quality and the increasing presence of alien species that are, in many cases, superior competitors in disturbed environments (Cadi and Joly 2003; Metzger et al. 2009).

In this study, the factors potentially influencing the presence of semi-aquatic reptiles in the fluvial systems of Girona (north-eastern Spain) were investigated. The lower reaches of the major rivers of the region have been subject to substantial habitat degradation, associated with watershed regulation and the widespread occurrence of alien species (Saurí et al. 2001; Ordeix et al. 2014). These changes have been associated with the collapse of native biotic communities in the coastal plain rivers (Doadrio 2001; Clavero et al. 2009). In contrast, the headwaters of the rivers are subject to greater seasonality, have been colonised by fewer alien species and constitute important shelters for native fauna (Boix et al. 2010; Maceda-Veiga et al. 2010).

In this region, four species of native semi-aquatic reptiles occur, including two turtles (*Emys orbicularis* and *Mauremys leprosa*) and two natricine snakes (*Natrix astreptophora* and *Natrix maura*; Pleguezuelos et al. 2002). Three of these species are widespread in the rivers of the region, but *E. orbicularis* is rare and localised (Mascort 1998). In addition, there is also an alien turtle, *Trachemys scripta*, which occurs occasionally in the rivers/streams of the region, particularly associated with disturbed parts of deltas and coastal marshes (Martínez-Silvestre et al. 2011). Therefore, interspecific interactions amongst the three species of turtles are likely to be localised, but could be common between the two natricines, which also show some overlap in their diets (Salvador 1998). In other European natricines, these associations can be negative or neutral, depending on the level of trophic overlap (Filippi et al. 1996; Scali 2011).

The widespread presence of alien species in the fluvial systems could influence the occurrence of the native semi-aquatic reptiles. However, it is not known what interactions occur between the native reptiles and alien species, because previous studies have focused only on the effects of alien species on native fish communities (Benejam et al. 2008; Clavero and Hermoso 2011). It is likely that native reptiles and alien species interact negatively, because they compete for similar prey (small fish, amphibians and macro-invertebrates; Doadrio 2001) and some alien fishes could be predators of the reptiles (e.g. *Esox lucius*, *Micropterus salmoides*; Lagler 1956; Zavala 1983).

In this study, the impact of alien species on the occurrence of the native reptiles was assessed and I expected that the effect would be negative (hypothesis i). My second objective was to assess whether the two natricines would show non-random associations, which I expect would be negative (hypothesis ii). My third objective was to identify the environmental characteristics of those river stretches that have greater diversity of semi-aquatic reptiles.

Methods

Study region

Based on the Köppen climate classification system, most of the study region has a *Csa* climate type (AEMET 2011) characterised by a warm dry summer. The headwaters of the Muga and Fluvià rivers are located in an area having a *Cfa* climate type (AEMET 2011), which is characterised by short periods of summer drought. The study involved seven fluvial systems having very distinct hydromorphological characteristics. These included: 1) the riera de Calonge, which is a seasonal stream of 3.5 km in length; 2) the Daró River, which is a seasonal stream of 35 km in length; 3) the Fluvià River (97 km in length and having a flow rate at the mouth of 11 $m^3 s^{-1}$); 4) the Muga River (58 km in length and having a flow rate of 3.3 $m^3 s^{-1}$); 5) the riera de Pedret, which is a seasonal stream of 17 km in length; 6) the Ter River (208 km in length and having a flow rate of 25 $m^3 s^{-1}$); 7) the Tordera river (62 km in length, and having a flow rate of 5.0 $m^3 s^{-1}$). The occurrence of alien species (alien fishes, crayfish) varies significantly amongst the basins of these rivers/streams (Ordeix et al. 2014). For example, alien species only occur at one site in the riera de Calonge (25%), while they were present in 96% of the sites in the Ter River (Suppl. material 1).

Sampling and habitat characterisation

Baited crayfish net traps (60 × 30 cm) were used to detect the presence of reptiles at 261 sites distributed amongst the six fluvial systems. The baiting method is commonly used in this type of study (Gibbons et al. 2006; McDiarmid et al. 2012). One to three traps separated by five metres were placed at each station for a period of 12–16 h. One end of each trap was suspended above the water to enable air breathing by the captured reptiles**.** The surveys were carried out between April and October 2016, encompassing the period of greatest activity for semi-aquatic reptiles in the region (Salvador 1998). This trapping method of capture is also effective in estimating the presence of fish and crayfishes (Johnson et al. 1992; Harper et al. 2002). The captured fishes were classified as alien species following Doadrio (2001).

The categorisation of riverine habitats was based on seven characteristics described by Pardo et al. (2002), including: 1) embeddedness in riffles and runs and sedimentation in pools; 2) riffle frequency; 3) substrate composition; 4) velocity/depth regime; 5) shading of river bed; 6) heterogeneity components; and 7) aquatic vegetation cover. The assessment of these characteristics enabled estimation of the heterogeneity of the riverine habitats, based on a fluvial habitat index (Pardo et al. 2002). High values of this index are associated with higher native biota diversity in Mediterranean fluvial systems (Pardo et al. 2002; Aparicio et al. 2011).

In addition to the above, the stream intermittency (or stream level) and the forest cover in the surveyed river sections were assessed. Stream levels were measured because

this is an important factor affecting the presence of alien species (Clavero and Hermoso 2011). The stream level was categorised as: 1) mild dryness (a small part dry); 2) moderate dryness (a large part dry); and 3) severe dryness (completely dry). Forest cover was assessed because of its effect on the biotic composition of the rivers (Gergel et al. 2002), including semi-aquatic reptiles (Ficetola et al. 2004; Escoriza and Ben Hassine 2017). The forest area was assessed by remote sensing-based habitat characterisation (Tuanmu and Jetz 2014). A range of major physicochemical parameters of waters was also measured (Eklöv et al. 1998; Peltzer and Lajmanovich 2004), including conductivity ($\mu S\ m^{-1}$), pH and dissolved oxygen ($mg\ l^{-1}$). These parameters were measured in situ, using a Crison 524 conductivity meter (for conductivity), an EcoScan ph6 (for pH) and a Hach HQ10 Portable LDO meter (for the dissolved oxygen content). The measurements of these parameters were made at a single time point between 11:00 h and 16:00 h (local time).

Data analyses

Data analysis was focused on investigating the relationships of the reptile occurrence to the various riverine habitat descriptors (i) and on patterns of reptile co-occurrence along the fluvial systems (ii). The presence of reptiles in relation to environmental conditions was visualised using canonical correspondence analysis (CCA) (Ter Braak 1986), which was conducted using the software package PAST 3.0 (Hammer et al. 2013). Significant associations between reptile occurrence and riverine habitat predictors were tested using distance-based linear models (DistLM), by developing a distance matrix using the Sørensen index for presence/absence data (Clarke and Gorley 2006). The significance was assessed following 9999 permutations of residuals under a reduced model (Clarke and Gorley 2006). To assess whether the predictors exerted a positive or negative influence on the dependent variable, XY scatter plots and trend lines were generated (Clarke and Gorley 2006). These analyses were carried out using PRIMER-E (PRIMER-E Ltd., Plymouth).

Co-occurrence patterns were investigated using joint species distribution models (JSDM) (Pollock et al. 2014). This method of analysis enables evaluation of whether the occurrence of a species is influenced by environmental factors and interspecific interactions. The finding of pairwise associations to the gradient superior to species' residual correlations is an indication that environmental filtering probably explained the co-occurrences of species (Pollock et al. 2014). On the other hand, the finding of strong residual correlations and weak associations with the gradient is as an indication that specific interactions probably explained the co-occurrences of species (Pollock et al. 2014). The model was adjusted by running five chains with 100,000 iterations each; the first 10,000 were discarded as burn-in and 10 was used as the factor to thin the post burn-in samples (Pollock et al. 2014). Model convergence was determined by Gelman-Rubin statistic (Gelman and Rubin 1996). These analyses were performed using R2jags (Su and Yajima 2011) and R (R Core Development Team 2017).

Results

During the surveys, four reptile species (*E. orbicularis*, *M. leprosa*, *N. astreptophora* and *N. maura*) were found, while the alien turtle species that also occurs in the study region was not detected. The presence of *E. orbicularis* was only observed in a single site (Fig. 1). For this reason, this species was included in the analyses, but not in the discussion of the results. The descriptive statistics for the environmental variables and species-sites are shown in Table 1. The data obtained for all the river basins and the list of observed or collected alien species are shown in Suppl. material 1.

The CCA showed the distribution of these reptiles as a function of the riverine habitats. The first axis of the CCA (eigenvalue = 0.24, explained variance = 56.86%) was negatively correlated with the presence of alien species and was positively correlated with stream level and fluvial index (Table 2 and Fig. 2). This axis described the transition between non-seasonal riverine habitats having greater/lesser alien species richness in coastal plain rivers/streams (Table 2 and Fig. 2). *Natrix astreptophora* and *N. maura* showed a positive association with this axis, while *E. orbicularis* and *M. leprosa* showed a negative correlation (Fig. 2). The second axis of the CCA (eigenvalue = 0.12, explained variance = 28.18%) was positively correlated with the stream level and was negatively correlated with altitude and the water conductivity (Table 2 and Fig. 2). This axis described the transition from mountain streams to seasonal plain

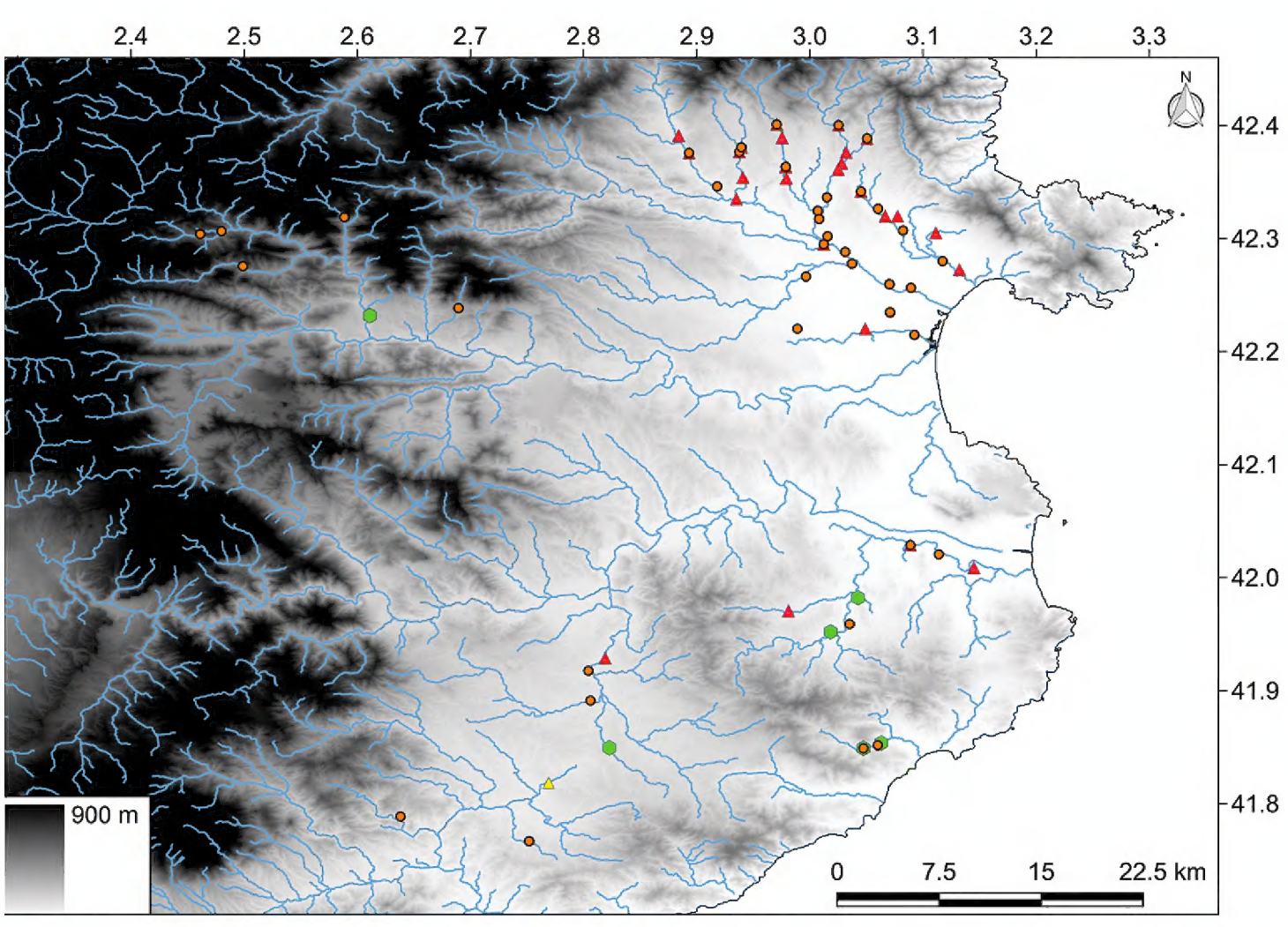

Figure 1. The study area, showing the distribution of sites, river basins and species. Yellow triangle: *E. orbicularis*; Red triangles: *M. leprosa*. Green circles: *N. astreptophora*. Orange circles: *N. maura*.

Table 1. Descriptive statistics (mean and range) of the environmental variables, including the total number of sites (*n*) with species presence. Conductivity, water conductivity (μS m^{-1}); Oxygen, Oxygen dissolved in water (mg l^{-1}); Alien fish, alien fish species richness.

	E. orbicularis	***M. leprosa***	***N. astreptophora***	***N. maura***
n	1	26	6	39
Altitude	72	61 (8–146)	71 (23–195)	108 (8–616)
Forest	67	35 (0–100)	27 (0–60)	32 (0–100)
Stream level	1.0	2.1 (1.0–3.0)	2.7 (2.0–3.0)	2.0 (1.0–3.0)
Fluvial index	40.0	55 (20–74)	63 (54–73)	54 (21–76)
Conductivity	538	371 (112–1129)	587 (278–1106)	490 (112–2335)
Oxygen	12.1	8.0 (2.5–12.6)	8.5 (5.2–9.9)	8.6 (1.1–17.8)
Water pH	8.6	7.8 (7.2–8.7)	8.1 (7.5–8.9)	7.9 (7.1–8.6)
Alien fish	1.0	1.3 (0.0–5.0)	0.0	1.0 (0.0–5.0)
Alien crayfish	1.0	0.9 (0.0–1.0)	0.5 (0.0–1.0)	0.7 (0.0–1.0)

Table 2. Results of the canonical correspondence analysis assessing the influence of the environmental gradient in the species occurrence. Eigenvalues and factor scores for the environmental variables are provided for the first two axes.

	Axis1	**Axis2**
Eigenvalues	0.244	0.121
Altitude	0.034	–0.195
Forest	–0.120	–0.022
Stream level	0.242	0.222
Fluvial index	0.222	0.125
Conductivity	0.140	–0.153
Dissolved oxygen	0.046	–0.101
Water pH	0.025	–0.081
Alien fish richness	–0.266	0.048
Alien crayfish	–0.241	0.141

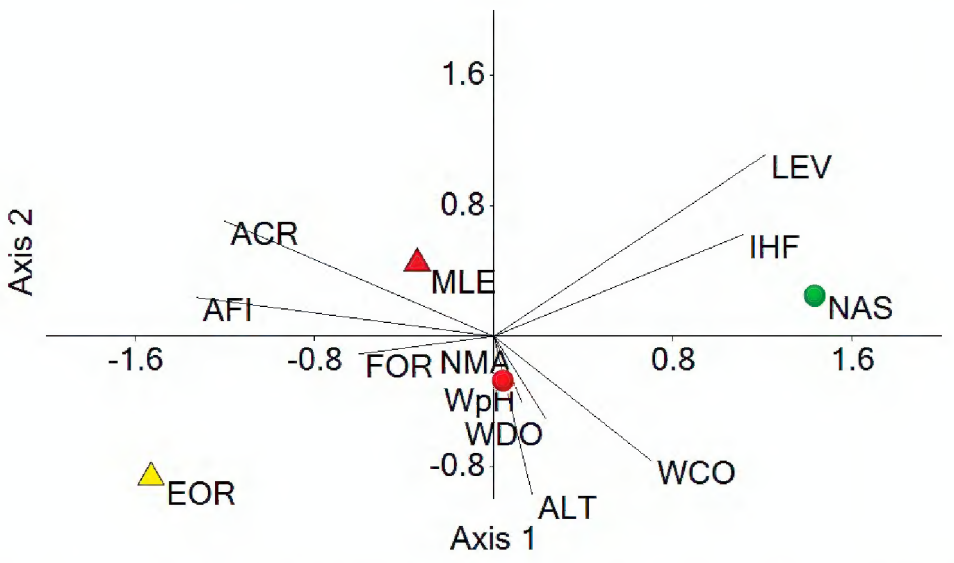

Figure 2. Canonical correspondence analysis scatter-plot of species and sites with the environmental variables fitted as vectors. ACR, alien cray fish presence; AFI, alien fish species richness; ALT, altitude; FOR, percentage of forest cover; IHF, fluvial habitat index; LEV, stream level; WCO, water conductivity; WDO, dissolved oxygen in water; WpH, water pH; EOR, *Emys orbicularis*; MLE, *Mauremys leprosa*; NAS, *Natrix astreptophora*; NMA, *Natrix maura*.

Table 3. Results of distance-based linear model testing for relationships between reptile presence and the environmental variables. +/– indicates the direction of the association. Significant values at $p \leq 0.1$ are shown in bold. Prop., proportion of explained variance.

	M. leprosa				*N. astreptophora*				*N. maura*			
	+/–	***F***	***p***	**Prop.**	**+/–**	***F***	***p***	**Prop.**	**+/–**	***F***	***p***	**Prop.**
Altitude	–	5.741	**0.016**	0.022	–	0.935	0.367	0.004	–	1.891	0.167	0.007
Forest	–	0.088	0.764	0.0003	–	0.411	0.546	0.002	–	0.862	0.346	0.003
Stream level	+	3.793	0.069	0.001	+	6.901	**0.012**	0.026	+	1.634	0.252	0.006
Fluvial index	–	0.067	0.801	0.0003	–	1.119	0.299	0.004	–	0.733	0.393	0.003
Conductivity	–	2.177	0.152	0.008	+	0.006	0.894	0.00002	–	0.905	0.325	0.003
Oxygen	+	0.353	0.549	0.001	+	0.482	0.466	0.002	+	4.066	**0.045**	0.015
Water pH	–	0.074	0.787	0.0003	+	1.341	0.248	0.005	+	0.031	0.859	0.0001
Alien fish	+	5.273	**0.024**	0.020	–	3.614	**0.074**	0.014	+	1.767	0.197	0.007
Crayfish	+	5.191	**0.025**	0.020	–	1.028	0.373	0.004	+	0.170	0.706	0.0007

Table 4. Pairwise environmental correlations obtained by a joint species distribution modelling.

	E. orbicularis	***M. leprosa***	***N. astreptophora***	***N. maura***
E. orbicularis	1.00 ± 0.00			
M. leprosa	0.45 ± 0.35	1.00 ± 0.00		
N. astreptophora	0.33 ± 0.30	0.41 ± 0.28	1.00 ± 0.00	
N. maura	0.51 ± 0.31	0.70 ± 0.20	0.37 ± 0.31	1.00 ± 0.00

Table 5. Pairwise residual correlations between species obtained by a joint species distribution modelling.

	E. orbicularis	***M. leprosa***	***N. astreptophora***	***N. maura***
E. orbicularis	1.00 ± 0.00			
M. leprosa	–0.11 ± 0.57	1.00 ± 0.00		
N. astreptophora	0.06 ± 0.57	–0.81 ± 0.22	1.00 ± 0.00	
N. maura	–0.23 ± 0.56	0.32 ± 0.15	–0.14 ± 0.32	1.00 ± 0.00

streams. The species that were positively correlated with CCA_2 were *M. leprosa* and *N. astreptophora*, while *E. orbicularis* and *N. maura* showed a negative correlation (Fig. 2).

The DistLM analysis indicated that the presence of *M. leprosa* was significantly negatively associated with altitude, but positively associated with alien fish richness and crayfish presence (Table 3). The occurrence of *N. astreptophora* was significantly positively associated with stream level, but negatively associated with alien fish richness (Table 3). The occurrence of *N. maura* was significantly positively associated with dissolved oxygen (Table 3).

The JSDM analysis showed a strong environmental correlation (R = 0.70) between *M. leprosa* and *N. maura*, while both natricine snakes showed a weaker correlation (R = 0.37; Table 4). There was a strong negative residual correlation in the occurrence of *M. leprosa* and *N. astreptophora* (R = –0.81), while *N. astreptophora* and *N. maura* showed a weak negative residual correlation (R = –0.14; Table 5).

Discussion

The fluvial systems of north-eastern Spain are highly disturbed and have been colonised by several alien species (Ordeix et al. 2014). Many studies have shown that alien species have a major impact on native icthyofauna and batrachofauna (Kats and Ferrer 2003; Cruz et al. 2008; Clavero and Hermoso 2011), but it is not known what effect they have on semi-aquatic reptiles. This uncertainty was investigated in the present study by analysing the patterns of presence of reptiles based on several environmental descriptors, including the presence of alien fishes and crayfish. The results showed that the presence of alien species also adversely affect the diversity of reptiles, although the species' vulnerability is variable.

The distLM analyses showed that the three species of semi-aquatic reptiles responded differently to the conditions of riverine habitats. *Mauremys leprosa* and *N. maura* occupied habitats in highly regulated coastal plain rivers having low structural diversity. Due to the stability of the watershed, these areas support a greater number of alien species that are poorly adapted to the Mediterranean seasonality (Benejam et al. 2005; Boix et al. 2010). The JSDM analyses also showed strong shared environmental responses between *M. leprosa* and *N. maura*, indicating that the co-occurrence of these species can be attributed to habitat filtering. The positive association of *M. leprosa* with highly disturbed stretches of the coastal plain rivers can be explained by several factors: (i) these populations of *M. leprosa* are close to the northern limit of the distribution of the species (Pleguezuelos et al. 2002) and their occurrence was negatively associated with altitude, which is a surrogate of the thermal gradient; (ii) this reptile shows heliothermic regulation (Salvador 1998) and occupies open, sun-exposed sections of the rivers. These sections have a lower fluvial habitat index score (Pardo et al. 2002); and (iii) *M. leprosa* is an opportunist feeder that includes alien species in its diet (Pérez-Santigosa et al. 2011), so it can thrive in habitats where native communities are very impoverished but alien species are abundant. *Natrix maura* also favours more stable river stretches that maintain water during the dry season. These sections typically retain populations of some small native fishes that are the usual prey for this snake (Salvador 1998). However, *N. maura* is a highly opportunistic predator and also feeds on alien fishes if they replace the native species (Rugiero et al. 2000).

By contrast, JSDM analysis indicated that there was a strong negative association between *M. leprosa* and *N. astreptophora*. The occurrence of *N. astreptophora* was positively associated with river sections having absence of alien fishes and higher hydrologic seasonality. Negative interactions between the two species are unlikely, as both differ in their use of habitats and trophic resources (Salvador 1998); this result might be caused by some non-evaluated habitat parameters (Börger and Nuds 2014). The association between *N. maura* and *N. astreptophora* was weakly negative, possibly caused by some trophic segregation, resulting in interspecific interactions being weak but not absent (Luiselli 2006).

Conclusion

Overall, the analyses indicated that the three species of reptiles can occur in altered river stretches (i.e. with low fluvial habitat indices). The semi-aquatic reptiles of the region are generalist species, well adapted to occupy highly dynamic habitats that show significant interannual fluctuations (Gasith and Resh 1999). In our study, most alien species are limnophilic species that have originated in regions with oceanic climates (Doadrio 2001); as a consequence, they are not well-adapted to the highly-variable discharge regimes that characterise Mediterranean-climate rivers (Boix et al. 2010). This fact suggests that restoring the natural flow regime could indirectly favour reptile diversity by creating hostile conditions for the persistence of alien species. In summary, the removal of alien species combined with habitat restoration measures to prevent future proliferation of alien species is probably the most appropriate strategy to preserve the diversity of native semi-aquatic species.

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Supplementary material 1

Supplementary tables

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Data type: habitat descriptive data

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